BioSystems 95 (2009) 82–87

Contents lists available at ScienceDirect

BioSystems

journal homepage: www.elsevier.com/locate/biosystems

Gaia again

Mahesh Karnani[a], Arto Annila[a,b,c,*]

[a] Department of Biosciences, University of Helsinki, FI-00014 Helsinki, Finland
[b] Institute of Biotechnology, University of Helsinki, FI-00014 Helsinki, Finland
[c] Department of Physics, University of Helsinki, FI-00014 Helsinki, Finland

ARTICLE INFO

Article history:
Received 13 May 2008
Received in revised form 8 July 2008
Accepted 9 July 2008

Keywords:
Energy transduction
Entropy
Evolution
Free energy
Homeostasis
Natural process
Natural selection
Organism

ABSTRACT

The ideas of the Gaia hypothesis from the 1960s are today largely included in global ecology and Earth system sciences. The interdependence between biosphere, oceans, atmosphere and geosphere is well-established by data from global monitoring. Nevertheless the theory underlying the holistic view of the homeostatic Earth has remained obscure. Here the foundations of Gaia theory are examined from the recent formulation of the 2nd law of thermodynamics as an equation of motion. According to the principle of increasing entropy, all natural processes, inanimate just as animate, consume free energy, the thermodynamic driving force. All species, abiotic just as biotic are viewed as mechanisms of energy transduction for the global system to evolve toward a stationary state in its surroundings. The maximum entropy state displays homeostasis by being stable against internal fluctuations. When surrounding conditions change or when new mechanisms emerge, the global system readjusts its flows of energy to level newly appeared gradients. Thus, the propositions of Gaia theory and holistic understanding of the global system are recognized as consequences of thermodynamic imperatives.

1. Introduction

The Gaia hypothesis (Lovelock, 1988; Lovelock and Margulis, 1974) by James Lovelock has been a subject of intensive debate. The bold hypothesis proposed that Earth is a giant organism where all living and nonliving entities interact and evolve together to maintain life on the planet. Today Gaia theory is largely recognized as an early vision of modern global ecology that voiced the interdependence between biota, oceans, atmosphere and geosphere. Lovelock was prompted to postulate a global homeostasis by the basic observation that Earth is unique among other planets in our solar system in having an atmosphere that has, for eons, been far from chemical equilibrium (Lovelock, 1972). It appears that all life on Earth regulates the living and nonliving environment so as to keep conditions such as ambient temperature and composition of the atmosphere and oceans suitable for life.

Like-minded views and evidence suggesting that Earth may be regarded as a gigantic organism had been expressed earlier by others (Lovelock, 1988; Kirchner, 2002), but the Gaia hypothesis reached a more wide-spread notoriety and generated a lively discussion about the definition of an organism and life in general. The Gaian ideas have been broken down into several different propositions (Kirchner, 2002; Barlow and Volk, 1992), of which some are perhaps regarded as lofty and ideological, whereas those more precisely formulated have been deemed scientific and testable. The central aspect of all of these is some form of self-regulation or homeostasis of the global system. Specific criticisms against the Gaia hypothesis have focused on the identity and nature of the mechanisms behind the global homeostasis. Indeed it has remained perplexing how global-scale cooperation could evolve from mutual competition that leads to natural selection of the fittest (Lenton, 1998; Barlow and Volk, 1992).

Considering the on-going climate change and other global environmental changes, it is time to inspect Gaia again in the light of the theory of evolution by natural selection (Darwin, 1859) that was recently founded on the thermodynamic principle of increasing entropy (Sharma and Annila, 2007). The fundamental formulation makes no distinction between animate and inanimate, but views all matter in motion as a result of energy transduction to diminish thermodynamic driving forces. Flows of energy channel down the steepest gradients. The thermodynamic imperative has been shown to be equivalent to the principle of least action that directs flows along the shortest paths (Kaila and Annila, 2008). The theoretical formulation has been used to account for the ubiquitous skewed population distributions of plants and animals, as well as genes and their sigmoid cumulative curves (Würtz and Annila, submitted for publication; Grönholm and Annila, 2007). Furthermore, the emergence of chirality consensus and other standards of life have been rationalized (Jaakkola et al., 2008a). The theory also tackles the

---

* Corresponding author at: Department of Physics, University of Helsinki, FI-00014 Helsinki, Finland. Tel.: +358 9 191 50629; fax: +358 9 191 50639.
E-mail address: arto.annila@helsinki.fi (A. Annila).

0303-2647/$ – see front matter © 2008 Elsevier Ireland Ltd. All rights reserved.
doi:10.1016/j.biosystems.2008.07.003

puzzle of large amounts of non-expressed DNA in eukaryotes (Jaakkola et al., 2008b). These recent findings are consistent with the results derived earlier from the maximum entropy principle (Brooks and Wiley, 1988; Lorenz, 2002; Salthe, 1993; Schneider and Kay, 1994; Ulanowicz and Hannon, 1987).

In this study it is clarified that the 2nd law of thermodynamics underlies Gaia theory. Thermodynamics is used to explain the nature and mechanisms of homeostasis in addition to giving definitions for an organism and for life in general.

2. Driving forces and flows

The 2nd law of thermodynamics (Carnot, 1924) was associated with the statistical imperative of increasing entropy by Boltzmann (1886) and of decreasing free energy by Gibbs (1993–1994). In accordance with this physical meaning, the concept of entropy is employed in this study as a measure of energy dispersal that obtains its maximum when all gradients of energy have vanished. To clarify the adopted standpoint, it is noted that the informational entropy defined by Shannon (1948) is not used here because it does not express entropy explicitly in terms of energy. The maximum entropy principle formulated by Jaynes (1957) builds on the informational entropy but aims at finding the paths that lead to increasingly more probable states. Thus, the principle of maximum entropy production for non-equilibrium stationary states (Dewar, 2003) parallels the thinking in this study where evolution is pictured to advance along the steepest ascents in entropy which are equivalent to the steepest descents in free energy. Thus, the theoretical framework used and the results presented here are not new as such but the 2nd law, now available as an equation of motion, can serve directly as the physical basis for the Gaia hypothesis.

Many processes in nature follow the principle of increasing entropy. For example, heat flows from hot to cold and molecules diffuse to dilute. Also, chemical reactions transform compounds k to other compounds j until the chemical potentials (Atkins, 1998) μ_k and μ_j have equalized. All these processes that level the thermodynamic driving forces are referred to as natural processes (Ho and Ulanowicz, 2005; Kondepudi and Prigogine, 1998). Flows of energy – be it by diffusion, convection, chemical reactions or any other process – are driven down along the potential energy gradients. This is the message of the 2nd law, equivalent to the principle of increasing entropy or the principle of decreasing free energy.

Entropy increases during evolution (Sharma and Annila, 2007; Kaila and Annila, 2008)

$$\frac{dS}{dt} = \sum_{j,k} \frac{dN_j}{dT} \nabla_k \frac{\mu_j}{k_B T} \geq 0 \tag{1}$$

when flows of matter $dN_j/dt = v_j$ diminish the driving forces $\nabla_k(\mu_j/kT)$ between potentials μ_j and μ_k. The transition from one state to another is accompanied with influx or efflux of energy. This is particularly evident in chemical reactions that are either endergonic or exergonic but applies also to transport phenomena (Kaila and Annila, 2008). In other words, only an open system is capable of evolving. When an influx of energy Q_j from the surroundings couples to the processes of the system, it is included in the driving force, typically as a divergence of vector potential. Entropy is the convenient statistical probability measure to keep track of all flows of energy. However, it is the energy gradients that generate and direct the probable flows of energy. Therefore the argumentation and its examples are mainly formulated in terms of energy flows rather than expressing it in terms of entropy production.

In the case of global climate (Paltridge, 1978), the kinetic energy of atmospheric gases increases when high-energy solar radiation heats the gas molecules and gives rise to prevailing winds, which are mechanisms for dispersal of energy down along global temperature gradients. Alike, ocean currents are voluminous conveyers of heat between the hot equator and the cold polar ice caps. Energy is dispersed further via various other transport and transformation processes to diverse repositories of energy, *e.g.*, populations of organisms. Finally, energy is dissipated as thermal radiation from Earth to its surroundings, here superficially referred to as the cold space. More precisely, the surroundings are heterogeneous and not equally transparent for all wavelengths (Matsuno, 2006).

In the case of chemical reactions, the thermodynamic gradient is customarily referred to as affinity $A_j = \mu_k + \Delta Q_{jk} - \mu_j$. It denotes the chemical potential difference between substrates and products. When external energy ΔQ_{jk} couples to the reaction, it adds to the substrate potential μ_k to yield products in non-equilibrium concentrations N_j, as in photosynthesis for example. Resulting high-energy chemical species fuel coupled reactions. According to the 2nd law given by Eq. (1), the biota has emerged in response to the high solar flux to conduct energy by numerous chemical transformation processes that also level mutual potential energy differences among populations. Thus, the biota is also an integral part of the global energy transduction machinery.

To describe sources of various flows, the energy content of each species, animate just as inanimate, is given by the potential $\mu_j = k_B T \ln[N_j \exp(G_j/k_B T)]$. For a biotic species, N_j is customarily referred to as population size and G_j as the trophic level height relative to the average energy $k_B T$. The potential μ_j signifies the thermodynamic cost to maintain the population N_j by the dissipative chain of energy transduction, which is customarily referred to as the food chain. Various cycles of matter result from the solar-energy powered assembly and the dissipation caused disassembly. The global system that comprises numerous potentials is pictured as an energy landscape (Kaila and Annila, 2008) in myriad motional modes, most of which are referred to as life. The manifold, given in Eq. (1) as time-dependent tangent vectors $\boldsymbol{v} \cdot \nabla$ (Prigogine, 1961; Lee, 2003), evolves toward a stationary state, with respect to its surroundings, that is largely governed, on one hand, by the hot Sun (*i.e.*, the source) and, on the other hand, by the cold space (*i.e.*, the sink). In the quest to attain a stationary state in its surroundings the global system has evolved over the eons to house a diversity of increasingly more effective mechanisms. The holistic view of nature through thermodynamics complies with the basic conservation laws of energy and momentum.

It is emphasized that evolutionary processes at all levels of hierarchy are flows of energy. They are directed by various thermodynamic gradients, defined as forces that are perceived either as attractive or repulsive. It is the mechanisms of energy transduction that are diverse and intricate—not the principle, which is ubiquitous and simple. Transport processes like diffusion will level spatial potential energy gradients due to temperature and concentration differences. Also an external field, such as an electric field, may couple to the transport resulting in electro-diffusion. Transformation processes such as chemical reactions will diminish potential differences by transforming entities k into j. When driven by an external electromagnetic field, the process is referred to as photochemistry.

In the global ecosystem the various thermodynamic forces generate numerous energy flows that are proportional to the thermodynamic gradients

$$v_j = \sum_k r_k \nabla_k \frac{\mu_j}{k_B T} \tag{2}$$

to be consistent with continuity (Sharma and Annila, 2007). As long as the potential difference $\nabla_k \mu_j / k_B T > 0$, the population of j may increase by transport processes and by transformation processes at the expense of other ingredients k in the system. On the other hand, when $\nabla_k\mu_j/k_BT<0$, N_j is in for a downsizing one way or the other to benefit other populations N_k.

The flow rate v_j is proportional to the mechanistic constant $r_k>0$. For example, energy may dissipate by a laminar flow or a turbulent transport mechanism. According to the 2nd law a hurricane is a mechanism that develops to funnel heat from tropical seas to the cold troposphere (Emanuel, 1991). Likewise, chemical reaction rates depend on transformation mechanisms such as catalysis. Upon closer examination, every mechanism can be regarded as a system of its own that emerged from an earlier natural process. For example, an organism is an entity of an ecosystem and also a system of its own that is composed of cells that, likewise, are systems of molecules. In other words, the global system has evolved toward increased dispersal of energy as numerous energy transduction systems have integrated into larger and larger systems. The criterion $\mathrm{d}S>0$ (Prigogine, 1961) is the general condition of integration. The energy transduction is self-similar, *i.e.*, a larger system is the surroundings for its subsystems. For example an ecosystem is the surroundings for each organism that in turn is the surroundings for its cells. The scale-independent thermodynamic description of energy transduction is applicable to all levels of hierarchy.

The diverse mechanisms are valued by their rates of entropy increase, *i.e.*, ability to diminish energy gradients. The rate has been recognized also earlier as the fitness criterion (Brooks and Wiley, 1988). Mechanisms that provide fast energy transduction, equivalent to fast rates of entropy increase or to the shortest paths, are favored. They are naturally selected (Sharma and Annila, 2007). Every time a new energy transduction mechanism emerges, evolution is punctuated by a rapid increase in the transduction. Later the natural process settles toward a stasis when the potential difference begins to be exhausted (Eldredge and Gould, 1972; Sneppen et al., 1995). The overall course is sigmoid. Initially the thermodynamic gradient is large, but the rate of evolution is limited by the newly emerged mechanistic capacity. When more mechanisms emerge, the flow of energy increases rapidly but later it slows down toward the stasis, being then limited by the nearly depleted gradient. At the stationary state all potential gradients driving changes in populations have vanished. There is no net-flux but through-flux powers numerous motions. A highly effective mechanism may emerge in response to a large potential but it will also require at the stationary state the large potential to supply the vital through-flux.

The characteristic sigmoid course of a natural process that may repeat itself over and over again, is often closely approximated by the biphasic form of the logistic equation (Strogatz, 2000). Also the law of mass action is often a good approximation for the flow equation (Eq. (2)) just as the Onsager reciprocal relations for cross correlated phenomena in the vicinity of the equilibrium and non-equilibrium stationary states (Kondepudi and Prigogine, 1998). Variations in potentials, as well as in mechanistic capacity, may trigger oscillations that are modeled by Lotka–Volterra equations. Obviously, the varying external flux drives annual and circadian oscillations. However, it is emphasized that these well-known and widely used analytical approximations for the flow equation (Eq. (2)) do not capture the fact that evolution is non-deterministic, *i.e.*, Eq. (1) cannot be solved analytically because flows consume the driving forces that, in turn, direct flows (Sharma and Annila, 2007). The arrow of time (Eddington, 1928), the sense of irreversibility, results from the influx or efflux of energy (Sharma and Annila, 2007). The open system acquires or loses energy. Even a small change in conditions at an early time point will affect the outcome at a later time. Thus, by definition (Strogatz, 2000), natural processes can even be chaotic.

3. The system characteristics

According to thermodynamics, all systems at all levels of hierarchy (*i.e.*, molecules, cells, organisms, etc.) are regarded as mechanisms of energy transduction. Obviously the amount of energy that is dissipated when, *e.g.*, a hydrogen bond forms is minute in comparison to the overall energy transduction of an organism. The scale is different, the principle, however, is the same.

Energy transduction systems will respond to internal and external changes by adjusting diverse μ_j, hence also N_j and G_j. Intensive interactions by effective mechanisms lead to a rapid adaptation, *i.e.*, re-dispersal of energy in response to the change in conditions. At the stationary state when all potential gradients $\nabla\mu_j$ are fully and efficiently in use by diverse mechanistic populations N_j, the resulting natural distributions of N_j are skewed, resembling log-normal distributions (Grönholm and Annila, 2007).

The maximum entropy non-equilibrium state corresponds to the free energy minimum at the maximum dissipation when the through-flux is at a maximum (Lotka, 1922). Often, an ecosystem at the maximum entropy state houses the highest number of different mechanisms to exhaust all available thermodynamic gradients. However, climax systems may reach the maximum dissipation with fewer highly effective species than were present during an earlier disparity (Gould, 1991). This is consistent with the thermodynamic imperative.

The imperative to equalize energy differences is sufficient to display homeostasis at the thermodynamic stationary state. The steady state, the stasis, is stable against internal fluctuations in the optimal populations N_j according to the Lyapunov stability criterion (Kondepudi and Prigogine, 1998; Strogatz, 2000) $\mathrm{d}S(\delta N_j)<0$, $\mathrm{d}S(\delta N_j)/\mathrm{d}t>0$. The homeostasis is a mere result of the quest for diminished gradients by maximal energy transduction to bring the system to the maximum entropy state. The mechanisms of homeostasis are the mechanisms of energy transduction. They are intrinsically interdependent by sharing the common constituents on Earth. In accordance with the postulation by Lovelock, the homeostasis is maintained by automatic and unconscious feedback mechanisms of the biota. Thermodynamics sees no difference between abiotic and biotic and no need for explicit controlled maintenance of a stable state as implied by the text-book definition of homeostasis (Cannon, 1932).

The global system is so large and subject to incessantly changing conditions (due to circadian, annual and solar rhythms, the Earth axis-nutation as well as due to more irregular motions such as plate-tectonics) that it is never quite in the stationary state. When the external flux changes, the system is bound to evolve toward a new, more probable state. Adaptation aims to attain the maximum entropy state with respect to prevailing circumstances. The response to the change in conditions leads to a revised optimal state. Small perturbations lead to small changes and thus the system appears homeostatic (Fig. 1). This is also the essence of Le Chatelier's principle, *i.e.*, external conditions command the state of chemical equilibrium. A small system, such as a bacterium, possesses few mechanisms of adaptation. The large global ecosystem houses many mechanisms of energy transduction to redirect its flows after changes in the external flux to attain the maximum entropy state. However, changes in conditions may be so dramatic that numerous mechanisms vanish abruptly and the system is not able to retain much of its prior energy transduction before powerful mechanisms have re-emerged. Current human endeavors are powerful energy transduction mechanisms consuming diverse sources of energy. Consequently other mechanistic species are endangered.

The thermodynamic principle is simple. When the energy density of a system differs from that of its surroundings, energy flows to reduce the difference. Often, but mistakenly, an animate entity

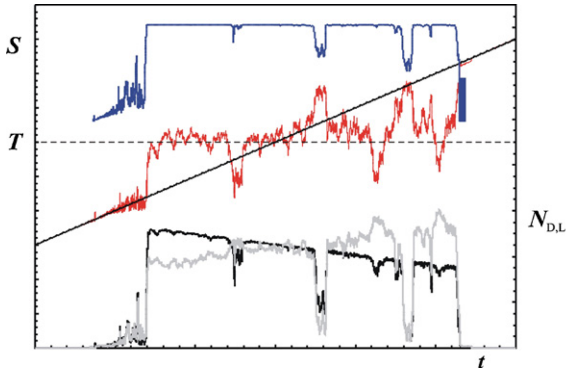

Fig. 1. Daisyworld simulation according to the principle of increasing entropy (Eqs. (1) and (2)). A planet of dark (D, black line) and light (L, grey line) colored daisies bathes in the radiation of a star whose luminosity (ΔQ) increases linearly with time t (solid line with a slope). The two shades of daisies have the same optimal growth rate $r(T_c)$ at temperature T_c (dashed line). However, the population (N_D) of dark daisies turns more of the absorbed radiation to heat, increasing ambient temperature whereas the population (N_L) of light daisies reflects more radiation, decreasing ambient temperature. Global temperature T (red) is modeled as a linear function of ΔQ, N_D and N_L. Initially ($t = 0$) the star was not luminous enough to warm the planet to the maximal energy transduction by daises which is signified by the low value of entropy (S, blue). Once some daises appeared due to random synthesis, the dark daisies began to dominate, because this led to the bias in T toward T_c facilitating the increase in entropy. At later times when the star became more and more luminous, the diversity of daisies turned from dark-dominated to light-dominated to maintain the energy transduction high even when the insolation tends to warm the planet above T_c. Random fluctuations caused 'ice ages' and 'warm periods' with concurrent decreases in populations and entropy. Finally, the star became too luminous to sustain energy transduction by the available mechanisms. All daisies died. Then the biotic energy transduction ceased and entropy of the biotic system fell accordingly. The asymmetry about T_c resulted from the increased synthesis at higher T and higher ΔQ. The daisyworld biota caused a substantial effect on planetary temperature in the quest for maintaining the high-energy transduction.

is viewed as being higher in energy than its surroundings. This may be true for its immediate surroundings but if this were true for the entire range that the animate entity is able to interact with, it would not find enough resources, *i.e.*, free energy, to continue to exist. The global system has evolved in the quest for a stationary state in its high-energy surroundings provided by the Sun. Mechanisms of energy transduction have emerged from the ingredients present on Earth and evolved over the eons to channel flows down along increasingly steeper gradients. Also within the global system all entities, *i.e.*, subsystems, are in relation to one and other via numerous flows according to Eqs. (1) and (2). Energy gradients power evolution and drive adaptation. This is the physical basis of the Gaia hypothesis.

4. Daisyworld simulation

Lovelock and Watson created the daisyworld simulation in a response to the argument that global homeostasis could only result through premeditated conscious cooperation of species (Watson and Lovelock, 1983). The simulation has been important in directing further development of Gaia theory. It shows how a simplified planetary system could unintentionally maintain a surface temperature suitable for its biota when the luminosity of the central star keeps increasing. Earth is clearly more complex than daisyworld, but analogously the output of our Sun has increased by 25% since the beginning of life and yet the surface temperature of Earth has remained rather stable (Newman and Rood, 1977). It is intensively being studied how organisms and the operations of man affect atmospheric composition by excreted substances, and influence temperature, *e.g.*, by the green house effect.

The evolution of a daisyworld was simulated using the principle of increasing entropy given by Eqs. (1) and (2) (Fig. 1). The self-consistent model is simple but it demonstrates that the essential features of Gaia theory are consequences of thermodynamics. The maximum entropy principle has been applied earlier in the context of daisyworld (as reviewed in Wood et al., 2008; Pujol, 2002), but using phenomenological rate equations rather than the fundamental flow equation (Eq. (2)) that is valid also far from equilibrium. Also cellular automata simulation has been used to show emergent self-regulation as a consequence of feedback coupling between life and its environment (Lenton and van Oijen, 2002), however, without establishing its thermodynamic basis. The simple model can be expanded and refined by including more terms in the master equation of evolution (Eq. (1)) and its flow equations (Eq. (2)) to include more mechanisms and to describe them in more detail. However, there is no need to include additional principles, *e.g.*, to simulate Darwinian processes.

The evolution was programmed as a for-loop of time steps. At each step, dark (D) and light (L) daises were randomly synthesized using Eq. (2) from base constituents in numbers N_1 according to a fixed stoichiometry (10:1) with the help of external energy ΔQ. The energy content of daisies was assigned 100 times larger than that of the basic constituents, *i.e.*, $G_D = G_L = 100G_1$. The rate of synthesis $r_{D,L} \propto \exp[(T - T_c)^2/2\sigma^2]$ about the set-point T_c of optimal growth was modeled as a Gaussian. The specific form is not important. For example, a quadratic form that has been used earlier yields similar results (Robertson and Robinson, 1998). The standard deviation σ defined the 'zone of life'. Temperature T of the planet was modeled to increase linearly with increasing ΔQ and with the population difference between N_D and N_L.

Earlier, the Stefan radiation law has been used to link the albedos of daisies with solar insolation. Indeed the Planck radiation law, which is also a consequence of the principle of increasing entropy leading to the equilibrium between radiation and matter, would be appropriate to model the temperature dependence. However, using the model with only the aforementioned parameters is deliberately simple to demonstrate the principle of decreasing free energy. After each time step, temperature, chemical potentials μ_1, μ_D and μ_L as well as the driving forces were updated. Large changes in μ_j within a step may trigger oscillatory behavior in analogy to chemical oscillations and animal population fluctuations. The fluctuations due to the random variation in syntheses were seen as 'glacial and warm epochs'. During the evolution T, N_D, N_L and entropy S were monitored but not used in any way to direct the course.

The particular choice of parameters corresponds to a specific 'planet' and another choice would result in different courses of evolution. Not every 'planet' will advance very far by its ingredients but all systems select, from emerging mechanisms, those that provide evolution the fastest rates of entropy increase and are able to maintain the high transduction of energy. In the daisyworld simulation other mechanisms than the dark and light daisies were not allowed to emerge from the random synthesis, however if additional mechanisms were to appear, the energy transduction and entropy would increase further. In this way by evolving mechanisms of energy transduction (Robertson and Robinson, 1998), the system aims at the stationary state in its surroundings. Furthermore, the observed thermostatic behavior (Fig. 1) is not an exclusive property of 'living' systems but, *e.g.*, simple physical resonance systems display similar phenomena as well (Oja et al., 1988).

5. Discussion

The thermodynamic account of the homeostatic global behavior provided here is not new as such. The connection between biological theory and thermodynamics has been established before (*e.g.*, Ulanowicz and Hannon, 1987; Brooks and Wiley, 1988; Collier, 1986; Schneider and Kay, 1994). In particular, the maximum entropy production principle has been used in attempts to understand Gaia theory (as reviewed in Wood et al., 2008; Kleidon, 2004). In general, the maximum entropy production principle is well-recognized as a powerful imperative to understand natural processes. However, it is also instructive to examine natural processes as energy dispersal. Eq. (1) links entropy to energy by identifying entropy increase as the result of flows of energy that decrease differences between thermodynamic potentials. Despite the concise notation, Eq. (1) is not a simplified but an extremely detailed formulation. The summations in Eq. (1) contain every unit of matter and every quantum of energy in the global system, making no distinction between animate and inanimate.

The consilience brought about by the principle of increasing entropy is inspiring. All processes at all length scales have the same motive of energy dispersal (Schneider and Sagan, 2005; Ulanowicz and Hannon, 1987; Brooks and Wiley, 1988; Collier, 1986; Schneider and Kay, 1994; Matsuno and Swenson, 1999). In accordance with Gaia theory and the classic texts of biological physics (Lotka, 1925) and ecology (Lindeman, 1942), thermodynamics makes no demarcation line between the living and nonliving. From the thermodynamic point of view, it is merely our choice to refer to those open systems that have evolved far from equilibrium by external-energy-powered chemical processes, as living organisms. In accordance with earlier thermodynamic argumentation (Lotka, 1925; Maynard Smith and Szathmary, 1999; Brooks, 2001), an organism is an open energy transduction system powered by external flux without further specifications about its mechanisms and modes of energy transduction. Obviously one may introduce further qualifications, *e.g.*, concerning ways of reproduction, to exclude Earth from the definition. The energy gradients experienced by the system direct its evolution. A new mechanism of energy transduction might emerge, *e.g.*, via random variation in the flows within the system or via inflows to the system. Any mechanism that will increase rates of gradient reduction, is naturally selected. Minor improvements direct paths along slightly steeper gradients, major evolutionary transitions open entirely new paths on the free energy landscape. From the thermodynamic viewpoint, life is a natural process powered by external flux without further conditions about its means and mechanisms.

Dissipative structures, *i.e.*, open non-equilibrium systems, may remain stable for long periods of time in a steady stream of external energy. These systems manifest autopoiesis, *i.e.*, they regenerate themselves recursively using the energy and matter flowing through them. The term autopoiesis (Maturana and Varela, 1980), self-production, is often regarded as a general characteristic of living organisms. Genetic mechanisms are highly effective means to instruct the re-emergence of metastable mechanisms to maintain a state of energy transduction, as well as to facilitate the emergence of novel mechanisms (Szathmary and Maynard Smith, 1997) that may eventually attain even higher states of energy transduction. However, it is emphasized that the surrounding densities in energy direct the overall process.

In the context of Gaia theory the term homeostasis is preferably replaced by homeorhesis (Waddington, 1957, 1968; Margulis, 1990) consisting of piecewise homeostases (Mamontov, 2007). The global system has evolved toward higher energy transduction by punctuations toward stases. These episodes have been particularly evident when the global biota has recovered from catastrophes. The trophic hierarchy has reappeared demonstrating that it is the surroundings that direct evolution, but with differing details, exemplifying the non-deterministic nature of evolution (Sharma and Annila, 2007).

The principle of increasing entropy, equivalent to decreasing free energy, is such a strong imperative that it will employ all mechanisms to its end. The non-equilibrium stationary state is attained and maintained by any means, giving the impression of regulation. This statement should not be interpreted to downplay the role of mechanisms. Not every planet contains the suitable mixture of ingredients and bathes in an appropriate energy flux that may couple to the ingredients to come up with an increasing diversity of increasingly more powerful mechanisms over the eons.

In summary, the physical basis of Gaia theory is in thermodynamics of open systems. This is not a new conclusion but is founded on the 2nd law given as an equation of motion. The holistic and scale-independent description of energy transduction, regards both the animate and inanimate as mechanisms to consume free energy. The quest to maintain high dissipation via frequent interactions manifests as homeostasis and adaptation without conscious regulatory mechanisms. The same incentive drives matter during evolution in increasingly more effective mechanisms by naturally selecting those among random variation that provide the highest rates of entropy increase. The global biota emerged over the eons in response to the solar-energy flux, and changed the global climate. Today the global economy is rising in response to the recently accessed contemporary energy supplies and is causing concurrent global changes. We should be thoughtful, in our brief quest for increased entropy by exhausting non-renewable resources, not to damage those vital mechanisms that have cumulated over the eons and would guarantee our existence also in the future (Diamond, 2005).

References

Atkins, P.W., 1998. Physical Chemistry, 6th ed. Oxford University Press, New York.

Barlow, C., Volk, T., 1992. Gaia and evolutionary biology. BioScience 42, 686–692.

Boltzmann, L., 1974. Populäre Schriften. Barth, Leipzig (1905). The second law of thermodynamics. In: McGinness, B. (Ed.), Ludwig Boltzmann, Theoretical Physics and Philosophical Problems, selected writings. Reidel, Dordrecht.

Brooks, D.R., Wiley, E.O., 1988. Evolution as Entropy: Toward a Unified Theory of Biology, 2nd ed. The University of Chicago Press, Chicago.

Brooks, D.R., 2001. Evolution in the information age: rediscovering the nature of the organism. Semiosis Evol. Energy Dev. 1, 1–26.

Cannon, W.B., 1932. Wisdom of the Body. W.W. Norton Co., New York.

Carnot, S., 1924. Reflections on the motive power of fire and on machines fitted to develop that power (1888). In: Mendoza, E. (Ed.), Reflections on the Motive Power of Fire—and other Papers on the Second Law of Thermodynamics by E. Clapeyron and R. Clausius. Dover Publications, New York.

Collier, J., 1986. Entropy in evolution. Biol. Phil. 1, 5–24.

Darwin, C., 1859. On the Origin of Species. John Murray, London.

Dewar, R., 2003. Information theory explanation of the fluctuation theorem, maximum entropy production and self-organized criticality in non-equilibrium stationary states. J. Phys. A: Math. Gen. 36, 631–641.

Diamond, J., 2005. Collapse: How Societies Choose to Fail or Succeed. Viking Books, New York.

Eddington, A.S., 1928. The Nature of Physical World. MacMillan, New York.

Eldredge, N., Gould, S.J., 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.J.M. (Ed.), Models in Paleobiology. Freeman, Cooper, San Francisco, pp. 82–115.

Emanuel, K.A., 1991. The theory of hurricanes. Annu. Rev. Fluid. Mech. 23, 179–196.

Gibbs, J.W., 1993–1994. The Scientific Papers of J. Willard Gibbs. Ox Bow Press, Connecticut.

Gould, S.J., 1991. The disparity of the burgess shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. Paleobiology 17, 411–423.

Grönholm, T., Annila, A., 2007. Natural distribution. Math. Biosci. 210, 659–667.

Ho, M.W., Ulanowicz, R., 2005. Sustainable systems as organisms? BioSystems 82, 39–51.

Jaakkola, S., Sharma, V., Annila, A., 2008a. Cause of chirality consensus. Curr. Chem. Biol. 2, 53–58.

Jaakkola, S., El-Showk, S., Annila, A., 2008b. The driving force behind genomic diversity. Biophys. Chem. 134, 232–238 (arxiv:0807.0892).

Jaynes, E.T., 1957. Information theory and statistical mechanics. Phys. Rev. 106, 620–630.

Kaila, V.R.I., Annila, A., 2008. Natural selection for least action. Proc. R. Soc. A., doi:10.1098/rspa.2008.0178.

Kirchner, J.W., 2002. The Gaia hypothesis: Fact, theory and wishful thinking. Clim. Change 52, 391–408.

Kleidon, A., 2004. Beyond Gaia: thermodynamics of life and earth system functioning. Clim. Change 66, 271–319.

Kondepudi, D., Prigogine, I., 1998. Modern Thermodynamics. Wiley, New York.

Lee, J.M., 2003. Introduction to Smooth Manifolds. Springer-Verlag, New York.

Lenton, T.M., 1998. Gaia and natural selection. Nature 394, 439–447.

Lenton, T.M., van Oijen, M., 2002. Gaia as a complex adaptive system. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 357, 683–695.

Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. Ecology 23, 399–418.

Lorenz, R.D., 2002. Planets, life and the production of entropy. Int. J. Astrobiol. 1, 3–13.

Lotka, A.J., 1925. Elements of Physical Biology. Williams & Wilkins, Baltimore.

Lotka, A.J., 1922. Natural selection as a physical principle. Proc. Natl. Acad. Sci. U.S.A. 8, 151–154.

Lovelock, J.E., 1988. The Ages of Gaia. Oxford University Press.

Lovelock, J.E., 1972. Gaia as seen through the atmosphere. Atmos. Environ. 6, 579–580.

Lovelock, J.E., Margulis, L., 1974. Atmospheric homeostasis by and for the biosphere—the Gaia hypothesis. Tellus 26, 2–10.

Mamontov, E., 2007. Modelling homeorhesis by ordinary differential equations. Math. Comp. Model. 45, 694–707.

Margulis, L., 1990. Kingdom animalia: the zoological malaise from a microbial perspective. Am. Zool. 30, 861–875.

Matsuno, K., Swenson, R., 1999. Thermodynamics in the present progressive mode and its role in the context of the origin of life. BioSystems 51, 53–61.

Matsuno, K., 2006. Forming and maintaining a heat engine for quantum biology. BioSystems 85, 23–29.

Maturana, H., Varela, F., 1980. Autopoiesis and cognition: the realization of the living. In: Cohen, R.S., Wartofsky, M.W. (Eds.), Boston Studies in the Philosophy of Science, vol. 42. Reidel D. Dordrecht.

Maynard Smith, J., Szathmary, E., 1999. The Origins of Life. Oxford Univ. Press, Oxford.

Newman, M.J., Rood, R.T., 1977. Implications of solar evolution for the Earth's early atmosphere. Science (New York, N.Y.) 198, 1035–1037.

Oja, A.S., Annila, A.J., Takano, Y., 1988. Resplitting of exchange-merged NMR absorption lines at high spin polarizations. Phys. Rev. B, Condens. Matter 38, 8602–8608.

Paltridge, G.W., 1978. The steady-state format of global climate. Q. J. Roy. Meteor. Soc. 104, 927–945.

Prigogine, I., 1961. Thermodynamics of Irreversible Processes. Interscience, New York.

Pujol, T., 2002. The consequence of maximum thermodynamic efficiency in daisyworld. J. Theor. Biol. 217, 53–60.

Robertson, D., Robinson, J., 1998. Darwinian daisyworld. J. Theor. Biol. 195, 129–134.

Salthe, S.N., 1993. Development and Evolution: Complexity and Change in Biology. MIT Press, Cambridge, MA.

Schneider, E.D., Kay, J.J., 1994. Life as a manifestation of the second law of thermodynamics. Math. Comp. Model. 19, 25–48.

Schneider, E.D., Sagan, D., 2005. Into the Cool: Energy Flow, Thermodynamics, and Life. The University of Chicago Press, Chicago.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, pp. 379–423 and 623–656.

Sharma, V., Annila, A., 2007. Natural process-natural selection. Biophys. Chem. 127, 123–128.

Sneppen, K., Bak, P., Flyvbjerg, H., Jensen, M.H., 1995. Evolution as a self-organized critical phenomenon. Proc. Natl. Acad. Sci. U.S.A. 92, 5209–5213.

Strogatz, S.H., 2000. Nonlinear Dynamics and Chaos with Applications to Physics, Biology, Chemistry and Engineering. Westview, Cambridge, MA.

Szathmary, E., Maynard Smith, J., 1997. From replicators to reproducers: the first major transitions leading to life. J. Theor. Biol. 187, 555–571.

Ulanowicz, R.E., Hannon, B.M., 1987. Life and the production of entropy. Proc. R. Soc. B 232, 181–192.

Waddington, C.H., 1968. Towards a theoretical biology. Nature 218, 525–527.

Waddington, C.H., 1957. The Strategy of the Genes. A Discussion of Some Aspects of Theoretical Biology. George Allen and Unwin, London.

Watson, A.J., Lovelock, J.E., 1983. Biological homeostasis of the global environment: the parable of daisyworld. Tellus 35B, 284–289.

Wood, A.J., Ackland, G.J., Dyke, J.G., Williams, H.T.P., Lenton, T.M., 2008. Daisyworld: a review. Rev. Geophys. 46.

Würtz, P., Annila, A., submitted for publication. Roots of diversity relations. J. Biophys.